

CHEMICAL CAMOUFLAGING AND BEHAVIORAL DEFENSES  
AGAINST A PREDATORY SEASTAR BY THREE SPECIES  
OF GASTROPODS FROM THE SURFGRASS  
*PHYLLOSPADIX* COMMUNITY

DEBBY A. FISHLYN AND DAVID W. PHILLIPS

*Department of Zoology, University of California, Davis, Davis, California 95616 U. S. A.,  
and Bodega Marine Laboratory, Bodega Bay, California 94923 U. S. A.*

The marine angiosperm *Phyllospadix* (surfgrass) commonly forms luxuriant beds in the lower rocky intertidal zone of the Pacific coast of North America. These beds provide a spatially heterogeneous substratum that supports a variety of inhabitants. Three conspicuous inhabitants of *Phyllospadix* beds along the coast of central California are the gastropods *Lacuna marmorata* Dall (a mesogastropod), *Alia carinata* (Hinds) (= *Mitrella carinata*; a neogastropod), and *Notoacmea paleacea* (Gould) (an archeogastropod). *Lacuna*, a herbivore, and *Alia*, an active, microcarnivore or scavenger, both occur widely on low intertidal rocks and algae, as well as on *Phyllospadix*. In contrast, the limpet *Notoacmea paleacea* occurs solely on *Phyllospadix* spp. This stenotopic limpet, which feeds directly on the epithelial layers of the surfgrass blade, possesses a striking series of morphological and behavioral adaptations for living on the narrow blades of surfgrass (Yonge, 1962; Fishlyn, 1976, and in preparation). Of particular interest here is the precise fit of the limpet's parallel-sided shell to the surfgrass blade, which enables the limpet to clamp down tightly on the blade surface if disturbed. All three gastropods are small: average size of *Lacuna* is about 4 mm, of *Alia*, about 8 mm, and of *Notoacmea*, about 6 mm.

The *Phyllospadix* beds provide a partial refuge against predation for these three small gastropods, and for other inhabitants, because the thin, floating blades are inaccessible to large, heavy, benthic predators such as the seastar *Pisaster ochraceus* (Brandt). However, the small (average diameter: 3 cm), agile seastar *Leptasterias hexactis* (Stimpson) is well suited for life on and among the blades of *Phyllospadix*, and it is a common resident of the surfgrass beds. In contrast to *Pisaster*, which possesses short, muscular tube feet, capable in concert of pulling apart its prey, *Leptasterias* possesses long, highly maneuverable (but relatively weak) tube feet. In the *Phyllospadix* beds, *Leptasterias* uses these tube feet to capture and ensnare small prey, which are then passed to the mouth. As the seastar moves along the surfgrass blade, the long tube feet are waved back and forth thus further extending the effective range of prey capture. Also occurring in surfgrass beds with *Leptasterias*, but far less frequently, is the larger seastar *Patiria miniata* (Brandt). *Patiria* is a particulate feeder and general omnivore (MacGinitie and MacGinitie, 1968; Sutton, 1975); it does not feed on live gastropods in the surfgrass beds. In contrast, *Leptasterias* is known to be an important predator of small gastropods when it occurs on rocky substrata (Menge, 1972).

Molluscan defensive adaptations against predators are manifested in many forms. Ansell (1969) has reviewed many of these adaptations and has classified them broadly as passive or active. Passive adaptations include morphological, physiological, and behavioral characteristics, such as the possession of a protective shell,

camouflage, or nocturnal foraging pattern. These may reduce predation but are not released by the immediate presence of the predator. Active adaptations, which are primarily behavioral, are released specifically by the presence of the predator. In the marine environment, active defensive adaptations often are triggered by chemicals (Feder and Christensen, 1966; Feder, 1972; Mackie and Grant, 1974; Phillips, 1978). Chemically-mediated defensive behaviors may be triggered by waterborne chemicals, emanating from distant predators, or they may be triggered by actual contact with the predator. Some gastropods give qualitatively different responses to distant predators (or to water "scented" by the predator) than they do to contact with the same predator (Szal, 1970; Phillips, 1975, 1977).

This paper examines defensive adaptations of *Lacuna*, *Alia*, and *Notoacmea*. Responses to waterborne chemicals emanating from the predatory seastar *Leptasterias* are described in the laboratory and in the field, as are responses to contact with this predator. A possible case of chemical camouflage is reported.

#### MATERIALS AND METHODS

All animals used in this study, except the limpet *Notoacmea insessa* (Hinds) were collected at low tide from *Phyllospadix scouleri* (Hooker) in Horseshoe Cove, adjacent to the Bodega Marine Laboratory, Bodega Bay, California. Specimens of *N. insessa* were collected nearby from stipes of the boa kelp *Egregia menziesii* (Turner) Areschoug. Animals were held in running sea water until use, which was within one week of collection. Preliminary behavioral observations were made during fall, 1976. Final behavioral experiments were conducted at the Bodega Marine Laboratory from October to December, 1978.

##### *Behavioral observations*

Responses to waterborne chemicals emanating from living seastars were examined initially in the laboratory. For these experiments, three kinds of test water were prepared, starting with 800 ml of sea water. Nothing was added to the first beaker, which served as a seawater control; one specimen of *Patiria miniata* (48.4 g wet weight) was added to the second; and 10 to 12 specimens of *Leptasterias* (11.0 g wet weight total) were added to the third. The three beakers were placed in a seatable and kept cold with running sea water (12° C) for approximately 2 hr before use. This procedure produced water "scented" by *Patiria* and *Leptasterias* (i.e., "scented water" or SCW). For experiments, gastropods were attached, or allowed to attach, to blades of *Phyllospadix scouleri*. Initially, attached snails were oriented in all directions (up, down, and sideways). Adjustments were made to position the snails in mid-blade areas, so they had equal opportunity to move up or down. Water to be tested was poured into a 600-ml beaker and let stand for 1 min. Then, the blades with attached animals were lowered vertically into the test water. Typically, 5 to 10 snails of one species were tested at one time using 5 blades of surfgrass mounted in a plastic holder that rested on the top of the beaker. A wide range of sizes of snails, from smallest to largest available, was used. Observations were made continuously for the first minute, and then at 1-min intervals for an additional 4 min. Data presented here are at the 3-min interval, because a substantial percentage of snails (*Lacuna* and *Alia*) began to move out of the beaker after 3 min.

Responses to contact with seastars also were examined in the laboratory. Snails were placed on a mat of *Phyllospadix scouleri* on the bottom of a shallow glass

bowl (20-cm diameter); the snails were covered with water, which was changed frequently. The *Phyllospadix* mat also was changed between testings of each species. Contact was made either with a blunt probe, tube feet of *Patiria miniata*, or tube feet of *Leptasterias hexactis*. Whole seastars were used, and two or more tube feet usually touched the gastropod. Responses were observed with a dissecting microscope mounted on a swing arm.

Field observations were made in Horseshoe Cove during lower low water in a large, surfgrass-filled, tide pool that received some flushing by waves even during minus tides. Individual *Leptasterias hexactis* were located *in situ*, and notice was taken of the behavior of snails on nearby surfgrass. Distances were measured between the seastar and the surrounding snails. Moving specimens of *Leptasterias* were followed, and the behavioral and predatory outcomes of contacts with snails were observed. After observations of an individual seastar in the tidepool, the seastar was turned over and examined to determine what it had been eating. Since *Patiria miniata* was not as common in the study area, encounters between snails and this seastar were staged by placing a seastar near cluster of snails.

### Biochemical analyses

Fresh samples of *Phyllospadix scouleri* (11 g), shells of *Notoacmea paleacea* (0.48 g), soft parts of *N. paleacea* (0.23 g), shells of *Notoacmea insessa* (0.50 g), and soft parts of *N. insessa* (0.46 g) were processed by standard techniques (Mabry, Markham, and Thomas, 1970; Harborne, 1973; Harborne, Mabry, and Mabry, 1975; Swain, 1976).

Specimens of *Notoacmea paleacea* were starved for 48 hr before use in order to clean the gut of residual plant material, and shells clean of epizoics were used. All samples (*Phyllospadix* and limpets) were macerated with mortar and pestle, initially at room temperature; then boiling 95% ethanol was added, and maceration continued. The tissue was extracted in ethanol overnight and centrifuged at 18,000 rpm for 30 min to remove precipitated proteins. The supernate was extracted with hexane to remove chlorophyll, carotenoids, and lipids. Samples of the alcoholic polar fraction were withdrawn for ultraviolet spectrophotometry and paper chromatography. Spectral data were obtained with a Perkin-Elmer 550 spectrophotometer operating over the range from 600 to 190 nm.

Two-dimensional, ascending paper chromatography was carried out using Whatman No. 1 paper. The first solvent was the upper phase of BAW (n-butanol: acetic acid: water, in a 4:1:5 ratio), and the second solvent was 15% acetic acid. Spots were visualized in daylight and under ultraviolet light (254 nm) before and after fuming with ammonia vapor. Selected spots were eluted in a small volume of 50% ethanol for 24 hr, and the UV spectrum of each eluate was determined.

## RESULTS

### Defensive responses of *Lacuna marmorata*

When specimens of *Lacuna marmorata* were placed in water from a beaker that previously had contained *Leptasterias hexactis* (i.e., *Leptasterias*-SCW), the snails' behavior changed dramatically from the resting state. *Lacuna* often reacted within 5 seconds of being placed in the stimulatory water, and within 30 seconds, all snails were reacting. Most commonly, the first response was to elevate the shell over the foot, a behavior aptly described as "mushrooming" by Bullock (1953) in reference to the defensive responses of another gastropod, the limpet *Collisella*

TABLE I

Responses of *Lacuna marmorata* to waterborne chemicals emanating from distant specimens of *Patiria* and *Leptasterias* in the laboratory. Snails were considered reacting if they rotated the shell and waved the cephalic tentacles within 3 min. Simultaneously, snails were scored for upward or downward movement without regard to whether or not they were showing shell-rotation behavior.

Stimulus	Number of snails		Number of snails		
	Reacting	Not reacting	Moving up	Moving down	Stationary
Control (N = 60)	0	60	1	0	59
<i>Patiria</i> (N = 60)	2	58	12	0	48
<i>Leptasterias</i> (N = 60)	60	0	19	3	38
<i>Leptasterias</i> (field) (N = 43)	41	2	—	—	—

*limatula*. Next, the shell and visceral mass began to swing violently back and forth through an arc of 360° while the two cephalic tentacles moved up and down rapidly and in unison. More than half of the reacting snails remained in place on the blade of surfgrass as they rotated the shell and waved their tentacles. The others ran, still twisting, and some of these climbed out of the water. This series of responses was also seen in the field when *Leptasterias* was nearby.

Two independent aspects of *Lacuna* behavior in control sea water, *Patiria*-SCW, and *Leptasterias*-SCW were examined quantitatively and are presented in Table I. These aspects are first, the number of snails that responded with shell rotation and tentacle waving, and second the number of snails that moved up, down, or remained stationary. In control sea water, none of the 60 snails tested responded with shell rotation or synchronous tentacle waving during the 3-min test period. In *Patiria*-SCW, 2 of 60 snails responded, and in *Leptasterias*-SCW, all 60 responded. A series of field observations of *in situ* *Leptasterias* confirmed the responses of *Lacuna* to *Leptasterias*: 41 of 43 specimens of *Lacuna* within 9 cm of seastars were responding with shell rotation and tentacle waving.

Directional movement along the blade of surfgrass was more frequent in seastar-scented water (Table I). Only 1 of 60 snails moved in control water, whereas 12 snails moved in *Patiria*-SCW ( $\chi^2 = 8.63$ ;  $P < 0.005$ ) and 22 moved in *Leptasterias*-SCW ( $\chi^2 = 21.52$ ;  $P < 0.001$ ). A greater number of snails moved in the presence of *Leptasterias* than in the presence of *Patiria* scent, but this difference, while probably real in light of the data on the shell-rotation response, was not statistically significant ( $\chi^2 = 3.32$ ;  $0.1 > P > 0.05$ ).

The combined response of *Lacuna* elicited by *Leptasterias* (i.e., shell-rotation, tentacle waving, and movement) differed markedly from that elicited by *Patiria*. Within the first 30 seconds of being placed in *Leptasterias*-SCW, all 60 specimens of *Lacuna*, although not yet moving, were vigorously twisting their shells and waving their cephalic tentacles; and within 1 min, 14 of the 60 specimens of *Lacuna* were rapidly moving. The response pattern in *Patiria*-SCW was very different: 6 snails were moving within the first minute, but none of these were reacting with shell rotation or tentacle waving; at 3 min, 12 were moving and 2 of these were reacting with very mild shell or tentacle movement; at 5 min, 12 were still moving but none of these were reacting.

The most frequent response of specimens of *Lacuna* to actual contact with *Leptasterias* was different from and more intense than the snails' response to the distant seastar or to seastar-scented water. Upon actual contact with *Leptasterias*, most of the snails would rear up on the posterior portion of the foot, raising their

TABLE II

*Responses of Lacuna marmorata to contact with seastars or a control probe in the laboratory and in the field. Two kinds of positive response were seen: rotating the shell (and, concomitantly, waving the cephalic tentacles) and falling off the Phyllospadix blade.*

Stimulus	Number of snails (laboratory conditions)			Number of snails (field conditions)		
	Rotating	Falling	Not reacting	Rotating	Falling	Not reacting
Control	0	0	20	0	1	39
<i>Patiria</i>	1	0	19	5	4	31
<i>Leptasterias</i>	6	14	0	6	68	1

cephalic tentacles as well, and fall off the *Phyllospadix* blade away from the point of contact. In the field, fallen snails often would hang by a mucous thread until they contacted a new blade of surfgrass. Then, they would attach to the new blade and move rapidly away while waving the cephalic tentacles and rotating the shell. Although falling was the most common response triggered by contact with the predator, some snails responded with a shell-rotation and cephalic tentacle response similar to that given when the predator was at a distance.

The responses of *Lacuna* to contact with a blunt probe, *Patiria*, and *Leptasterias* are quantified in Table II. Experiments were performed in the laboratory and in the field. All 20 snails tested in the laboratory responded to a light touch with a blunt probe by withdrawing briefly and then by resuming normal activity (*i.e.*, no reaction). No shell-rotation or falling responses were elicited. Similarly in the field, 39 of 40 snails showed no reaction to the probe; 1 snail fell from a surfgrass blade. Contact with *Patiria* elicited a more vigorous response by some of the snails. One snail of 20 in the laboratory responded to *Patiria* with shell rotation; and in the field, 9 of 40 responded in some fashion (5 with shell rotation and 4 by falling). In contrast, almost all of the snails responded vigorously upon contact with *Leptasterias*. All of the 20 snails in the laboratory responded (14 by falling); and in the field, 74 of 75 snails responded (68 by falling). The proportion of snails responding to *Leptasterias* in the field (99%) was far greater than the proportion responding to *Patiria* (22%).

*Lacuna*, then, has two sets of defensive responses, and the distance between the snail and the predator determines which set will be triggered. As a distant *Leptasterias* approaches, the snail becomes alerted and begins to explore with its cephalic tentacles. At the same time, the snail begins to rotate its shell back and forth through an arc of 360°. This response may lessen the ability of the seastar's tube feet to attach to the shell should contact occur, and it also exposes more of the sensory area of the snail's foot. The general activity level of the snail increases, and some individuals may avoid the approaching predator by moving away. If physical contact is actually made with the seastar, the snail tries to escape by falling off the blade.

#### *Defensive responses of Alia carinata*

The responses of *Alia carinata* to *Leptasterias*-SCW were not dramatic. There was no twisting of the body nor waving of the cephalic tentacles. There did seem to be a slight increase in general activity over control levels, but we do not have quantitative data to support this impression. There was, however, one clear

TABLE III

Responses of *Alia carinata* to contact with seastars or a control probe in the laboratory and in the field. All positive reactions (rearing, running, falling, and biting) are combined.

Stimulus	Number of snails (laboratory conditions)		Number of snails (field conditions)	
	Reacting	Not reacting	Reacting	Not reacting
Control	0	20	2	30
<i>Patiria</i>	0	20	1	29
<i>Leptasterias</i>	20	0	23	8

indication that *Alia* was detecting the presence of *Leptasterias*-SCW. When snails were placed in *Leptasterias*-SCW, the tip of the snails' siphon flared almost immediately, and did so in all 20 trials. Furthermore, when *Leptasterias* was actually present nearby, *Alia* often pointed its siphon toward the seastar. Although flaring of the siphon is not itself a defensive response, it indicates that the snail is detecting the presence of the predatory searstar. No siphon flaring occurred in 20 trials with *Patiria*-SCW or with control water.

Definite defensive responses were demonstrated by most specimens of *Alia* upon contact with *Leptasterias* in the laboratory and in the field (Table III), but specifics of the responses varied between individuals. In the laboratory, contacts with the snail's siphon most often resulted in *Alia* rearing up on the posterior portion of its foot. With its anterior end thus elevated and with the posterior tip of the foot fixed in place, the body twisted through an arc of 180° away from the point of contact. The snail's pointed shell was then quickly rotated to a position perpendicular to the body, where it remained, exposing the most body tissue (and perhaps coincidentally the sharp operculum) toward the seastar. Snails then ran rapidly away with the siphon flared and pointed toward the seastar. Running in response to *Leptasterias* was accomplished by a muscular, inching movement of the slender foot, in contrast to the smooth, gliding motion characteristic of the snail when it was not reacting.

All 20 snails in the laboratory reacted to *Leptasterias* in some way. In the laboratory, 8 of 20 trials began with the rearing response and concluded with the snail running from the seastar. In the remaining 12 trials the snail reared and began to run, but then either fell off the blade of surfgrass (3 trials) or struck at the seastar with its proboscis (9 trials). These additional responses generally occurred when the seastar continued to contact the snail after the snail had attempted to run. Snails that fell from the *Phyllospadix* blade remained attached by a mucous thread, which they later could climb to return to the blade from which they had fallen. Proboscis strikes were aimed at the tube feet of the attacking seastar with remarkable accuracy. Further, the snail's proboscis, which is as long as its body, was able to bite tube feet approaching from any direction, including the posterior. When bitten by the snail, the individual tube feet of the seastar recoiled immediately, and, if they were attached to the shell, they released their grip. The snail's proboscis would then sweep over the shell surface, as if to check for the presence of remaining tube feet.

The contact responses were given selectively to *Leptasterias* (Table III). In the laboratory, none of 20 snails responded to contact with a blunt probe; and in the field, 2 of the 32 snails tested were scored as having given positive responses

when they fell from the plant blade. In the laboratory, none of 20 snails responded to contact with *Patiria*; and in the field, 1 of 30 snails fell from the plant blade. No proboscis strikes were observed against *Patiria*. By contrast, responses were triggered upon contact with *Leptasterias* in a high proportion of trials. In the laboratory, 100% of the snails ( $N = 20$ ) responded in some fashion; and in the field, 74% ( $N = 31$ ) responded.

#### *Defensive responses of Notoacmea paleacea*

No difference was noted in the behavior of *Notoacmea paleacea* in control water, *Patiria*-SCW, or *Leptasterias*-SCW (20 trials each). In the laboratory, none of the 40 limpets examined in seastar-scented water showed any behavior that could be considered unusual; few (12.5%) moved at all during the 3-min test period. Similarly, field observations on 20 *in situ* limpets indicated that no macroscopic behavioral response was elicited by nearby *Leptasterias*.

Specific responses to contact with *Leptasterias* also were absent. When contacted by a blunt probe in the laboratory ( $N = 20$ ), the consistent response was to withdraw the soft body parts and to clamp down on the blade for a few seconds. Similarly, when contacted by a tube foot of *Patiria* ( $N = 20$ ) or *Leptasterias* ( $N = 20$ ), the body parts were withdrawn and the shell was clamped tightly to the blade. Field observations on 20 *in situ* limpets gave the same result. Neither mushrooming, running, nor twisting of the shell were ever observed after contact. After clamping down, the limpets remained motionless as the seastar crawled over them.

#### *Incorporation of specific chemicals from Phyllospadix by Notoacmea paleacea*

The curious lack of a behavioral response to *Leptasterias*, coupled with the fact that *Notoacmea paleacea* is known to consume the *Phyllospadix* on which it resides (Test, 1945; Fritchman, 1961; Fishlyn, 1976; Barbour and Radosevich, 1979; Fishlyn, in preparation) suggested that the limpet might be incorporating into its shell or tissues ingested plant chemicals that might act in a form of chemical defense. These chemicals might serve as camouflage, or they might render the limpet distasteful. If *N. paleacea* is incorporating specific chemicals from *Phyllospadix*, then other limpets not feeding on *Phyllospadix* should not contain those chemicals. For comparison, we examined specimens of *Notoacmea insessa*, a stenotopic limpet that feeds on the boa kelp *Egregia menziesii*, a brown alga. We chose *N. insessa* for comparison because it possesses a brown shell as does *N. paleacea*, and it occurs in a similar environment. D. Lindberg (personal communication) states that "*Notoacmea*" *insessa* is not a true *Notoacmea* and properly belongs in another genus.

An alcoholic extract of *Phyllospadix scouleri* blades was a deep, yellow-amber color after treatment with hexane, and a similarly-treated extract of macerated, epizoid-free shells of *N. paleacea* also was yellow in color. Since hexane treatment would have removed the relatively nonpolar pigments (such as chlorophyll and carotenoids), flavonoid pigments, which are relatively polar, were implicated as the most likely source of the color of both extracts. Flavonoids are known to be present in *Phyllospadix* (Nissen and Benson, 1964; S. Brauner, personal communication). In contrast to the yellow color of extracts of *Phyllospadix* and *N. paleacea* shells, alcoholic extracts of the bodies of *N. paleacea* and *N. insessa* were green, and extracts of the shells of *N. insessa* were colorless.

Crude alcoholic extracts (after hexane treatment) of *Phyllospadix* and *N. paleacea* shells were applied as spots to chromatography paper and were easily detected under UV light (254 nm). The spots appeared as dark-absorbing centers surrounded by fluorescing blue-green rings, indicating the presence of phenolic compounds such as flavonoids (Mabry *et al.*, 1970; Harborne, 1973). In contrast, samples of *N. paleacea* bodies, *N. insessa* bodies, and *N. insessa* shells could not be detected on chromatography paper under UV light either before or after fuming with ammonia vapor. The absence of detectable spots after ammonia fuming indicated that phenolic compounds were probably absent from these extracts (Mabry *et al.*, 1970; Harborne, 1973).

Gross spectral features of the crude extracts of *Phyllospadix* and limpet bodies and shells were then examined with a UV spectrophotometer. The extracts of *Phyllospadix* and *N. paleacea* shells absorbed strongly in the 300-nm region and had approximately similar UV spectra. In contrast, extracts of *N. paleacea* bodies and *N. insessa* bodies and shells differed significantly from the spectra of *Phyllospadix* and *N. paleacea* shells. In particular, these extracts did not absorb appreciably in the 300-nm region. Strong absorbing peaks in the 300-nm range are characteristic of flavonoids and simpler phenolic compounds (Harborne, 1973; Harbone *et al.*, 1975; Mabry *et al.*, 1970; Swain, 1976).

The characteristics of the crude extracts suggested that similar phenolic compounds were present in *Phyllospadix* and in the shell of *N. paleacea*. Since these chemicals were not present in detectable amounts in the shell or body of *N. insessa*, incorporation of these plant chemicals into the shell of *N. paleacea* also was suggested.

To further characterize the extracts of *Phyllospadix* blades and *N. paleacea* shells, samples were applied to chromatography paper and developed in two dimensions, first with BAW and then with 15% acetic acid. Two-dimensional chromatography of the extract of *Phyllospadix* produced nine distinct spots detectable under UV light. Four were arrow-shaped, brown, absorbing spots under UV, and each of these turned a more intense yellow-brown when fumed with ammonia vapor. These four spots were colorless in daylight before fuming with ammonia vapor, but all four became a deep yellow after fuming. Two other spots were fluorescent blue under UV. These became a more intense blue after fuming with ammonia vapor. Two more were a fluorescent green under UV, and another was a fluorescent blue-green. The color of all three intensified after fuming with ammonia. All nine spots isolated from the plant extracts are likely to represent either flavonoid pigments (sulphated flavones) or simpler phenolic compounds (*e.g.*, cinnamic acids).

Chromatography of the extract of *N. paleacea* shells produced two distinct spots. Under UV light, one was an arrow-shaped, brown, absorbing spot that turned a more intense yellow-brown after fuming with ammonia. In daylight, this spot was colorless before fuming with ammonia and yellow afterwards. The second spot was a fluorescent blue-green under UV. The color intensified after fuming.

One of the two spots from the extract of *N. paleacea* shells (the brown absorbing spot) closely matched in position, color, shape, and UV spectrum one of the spots from the extract of *Phyllospadix*. The spot from the limpet extract had an  $R_f$  value of 0.21 in BAW and 0.75 in acetic acid; the analogous spot from the plant extract had an  $R_f$  value of 0.23 in BAW and 0.71 in acetic acid. Before fuming with ammonia, both were colorless in daylight and brown under UV. After fuming, both were yellow in daylight and an intense yellow-brown under UV.



Both spots were arrow-shaped. Finally, the UV spectra of extracts of the two spots were similar. An extract of the limpet spot had absorption peaks at 332 and 269 nm (in 50% ethanol). An extract of the analogous plant spot had peaks at 333 and 275 nm. These data identify both chemicals as flavonoids (probably sulphated flavones), and the close match of physical properties suggests that they differ very slightly, if at all. In addition, the presence of arrow-shaped, dark, absorbing spots with low mobility in BAW and high mobility in aqueous acetic acid approximates properties of sulphated flavonoids found in the eelgrass *Zostera* by Harbone (1975).

The second spot from the extract of *N. paleacea* shells did not have an obvious analog in the extract of *Phyllospadix*. The  $R_f$  value of this fluorescent blue-green spot from the limpet extract was 0.35 in BAW and 0.30 in acetic acid. A similarly colored spot was not apparent in this position on chromatograms of plant extract; however, that position on the plant chromatograms was surrounded by three intense, brown, absorbing spots, and these may have masked its presence. Spectral analysis on an extract of the fluorescent blue-green spot indicated a shoulder at 320 nm, another shoulder at 270 nm, and a peak at 242 nm. This spot may represent another flavonoid, or, perhaps more likely, a simpler phenolic acid (e.g., cinnamic acid).

*Effectiveness of the defensive adaptations of Lacuna marmorata, Alia carinata, and Notoacmea paleacea*

The behavioral responses of *Lacuna* and *Alia* are presumed to be defensive adaptations against predation by seastars, and the incorporation of plant chemicals by *N. paleacea* may also function defensively by providing chemical camouflage against predatory seastars. The effectiveness of these adaptations in reducing predation is difficult to assess, but observations on the outcome of encounters between predator and prey provide some information. For instance, encounters involving contact between *Lacuna* and *Leptasterias* were observed on 75 occasions in the field. Eight of these encounters resulted in the capture of the snail; 67 encounters (89%) resulted in the escape of the prey from the predator. If it is assumed that the predator would eat a snail if it could capture it, then one might say that the combined defensive responses of *Lacuna* were 89% effective in reducing predation under the conditions existing in the field site that was studied.

While the defensive responses of *Lacuna* seemed to be fairly effective (i.e., 89% effective), the defensive responses of *Alia* seemed even more effective. Once tube feet of the predator had attached firmly to the shell of *Lacuna*, this snail rarely escaped being eaten. In contrast, the biting response of *Alia* forced the release of any attached tube feet, and sometimes tube feet even were dislodged without the biting response when *Alia* rotated its shell. Often in the laboratory, it was the predator that finally retreated from the prey, and in the field, none of the 31 encounters observed between *Alia* and *Leptasterias* resulted in the capture of the prey. As a further example of the effectiveness of the defensive responses of *Alia*, 4 specimens of *Leptasterias* were maintained in an aquarium with 20 specimens of *Alia* and a small *Phyllospadix* plant for 3 weeks without any of the snails being eaten.

In the *Phyllospadix* beds, the passive defense (*sensu* Ansell, 1969) of *Notoacmea paleacea* also seemed to be more effective in reducing predation than the behavioral defense of *Lacuna*. Twenty encounters between *N. paleacea* and

*Leptasterias* were observed in the field, and none resulted in the capture of the limpet. A further indication of the relative effectiveness of the defenses of *N. paleacea* and *Lacuna* is found in the diet of *Leptasterias* in the *Phyllospadix* beds.

Over a 2-year period (1976–78), 142 feeding seastars were examined, and most were eating *Lacuna*. In fact, specimens of *Lacuna* comprised 96.2% of the total numerical diet (418 prey total) and 97.1% of the gastropods taken (414 gastropods). Specimens of *N. paleacea* accounted for only 1.4% of the gastropods taken; *Alia* accounted for 0.5%, and two other gastropods, the limpet *Collisella pelta* (juveniles) and the snail *Lirularia succincta*, accounted for 0.7 and 0.2% respectively. Although *Lacuna* certainly is abundant in the *Phyllospadix* beds, this extremely high proportion of *Lacuna* in the diet did not fit our perception of the relative abundance of the three gastropod species in the beds. Consequently, four random samples of *Phyllospadix* from around feeding specimens of *Leptasterias* (575 g total blade wet weight; rhizomes removed before weighing) were taken near the study area in December, 1978. The resident specimens of *Lacuna*, *N. paleacea*, and *Alia* were counted, and a total of 410 individuals of *Lacuna*, 274 of *N. paleacea*, and 46 of *Alia* were found. The relative abundance of these gastropods on the surfgrass samples (60.1, 33.8, and 6.1% respectively) differed significantly from their relative abundance in the predator's diet (97.1, 1.4, and 0.5% respectively). *Lacuna* was indeed the most abundant prey available to *Leptasterias*, but it was present in the predator's diet in significantly greater numbers than would have been expected if prey were taken at random. Conversely, specimens of *N. paleacea* were significantly underrepresented in the predator's diet. We have interpreted these data on relative abundance as indicating a more effective anti-predator defense by *N. paleacea*. However, it should be mentioned that our data, like other data of this sort, could be interpreted alternately as indicating a preference of the predator for *Lacuna* over *N. paleacea*. Moreover, our population sample (taken once in winter) does not fully complement our feeding observation samples (taken over different seasons spanning two years). Nonetheless, the fact is that the diet of *Leptasterias* seems to be nonrandom with respect to *Lacuna*, *N. paleacea*, and *Alia*. The behavioral cause of this nonrandomness could be prey defenses or predator preferences or a combination of the two.

#### DISCUSSION

Vigorous defensive responses were given to the predatory seastar *Leptasterias hexactis* by two inhabitants of the *Phyllospadix* beds, *Lacuna marmorata* and *Alia carinata*. Both of these gastropods are capable of sensing the predator from a distance by means of waterborne chemicals, and also upon contact. Furthermore, these defensive responses are given relatively specifically in that they tend not be given to *Patiria miniata*, a seastar that is not a predator on mollusks. Species specificity was not complete, however, because *Patiria* did trigger a small percentage of weak responses. A similar low proportion of weak defensive responses to *Patiria* also was reported for the gastropods *Olivella biplicata* and *Collisella limatula* (Phillips, 1976, 1977).

The response of the mesogastropod *Lacuna marmorata* to distant *Leptasterias* involved rotation of the shell, tentacle waving, and increased general activity. All of these are common components of defensive responses of other gastropods, primarily of archeogastropods (Feder, 1963; Montgomery, 1967; Szal, 1970; Hoffman and Weldon, 1978). One difference, however, is that rotation of the shell previously has been associated most often with responses to contact with the predator.

In contrast, *Lacuna* begins rotating its shell when the predator is still some distance away, presumably in preparation for anticipated contact. Then, upon contact with *Leptasterias*, *Lacuna* reacts by falling away from the seastar, often escaping into the heterogeneous "jungle-like" mat of surfgrass blades. Falling as a defensive response also has been reported by Dayton, Rosenthal, Mahen, and Antezana (1977) who reported taxonomically various prey falling from, or being swept from, rocks as part of their response to the predatory seastar *Meyenaster gelatinosus*. These authors considered falling to be an effective means of escape from this seastar, and they noted that the degree of effectiveness was increased by conditions of strong surge. As the name surfgrass suggests, *Phyllospadix* flourishes in relatively high-energy environments, and while we have not observed wave surge to aid *Lacuna* in its escape from *Leptasterias*, some benefit may be gained from this by *Lacuna* at high tide. It also should be noted, however, that falling may be hazardous, as the direction and depth of the fall cannot be precisely controlled by the snail. Thus, for example, one of us (DAF) once watched a specimen of *Lacuna* fall away from a specimen of *Leptasterias* only to land on the oral tentacles of the sea anemone *Anthopleura xanthogrammica* and be engulfed.

Our subjective characterization of these defensive responses of *Lacuna marmorata* is that they are vigorous and dramatic. This conflicts, however, with the one previous mention of defensive responses by *Lacuna*. Menge (1972), in a study of the feeding biology of *Leptasterias hexactis*, noted that a defensive response was given by *Lacuna* sp. to this seastar. The response was not described in detail, but it was characterized as weak, while responses of several other gastropods familiar to us were characterized as strong or very strong. There are several possible explanations for the differences between our results and those of Menge (1972): different experimental conditions were used (e.g., in our experiments the snails were attached to blades of *Phyllospadix*), different species of *Lacuna* may have been examined, and different species of *Leptasterias* may have served as the stimulus. This latter possibility is particularly noteworthy since it pertains to results with other gastropods as well. Chia (1966) has synonymized *Leptasterias hexactis* and *Leptasterias aequalis* in Washington State based on specimens from the San Juan Islands, Washington, and this synonymy was extended to species of *Leptasterias* in California (Sutton, 1975) without published evidence (J. T. Carlton, personal communication). There is a distinct possibility that the *Leptasterias* that occurs on *Phyllospadix* in central California is a different species from the *Leptasterias* studied by Menge that occurs on rocks in Washington.

In contrast to the flight responses of *Lacuna* and most other gastropods, the response of *Alia* to *Leptasterias* is much more aggressive. Although *Alia* may flee from *Leptasterias* upon initial contact, if contact with the seastar persists, the snail quickly becomes combative and strikes at the seastar with its proboscis. Often after a series of such defensive strikes, it is the predator that withdraws. This sort of defensive counter-attack has been reported relatively infrequently in mollusks, but Pratt (1974) has reported that the mesogastropod *Crepidula fornicata* jabs with its radula when attacked by the oyster-drill *Urosalpinx cinerea*. Although the proboscis strike of *Alia* is elicited relatively specifically in that it is triggered by *Leptasterias* but not by *Patiria*, we have also seen *Alia* strike at other *Alia* and occasionally at *Lacuna*.

Whereas *Lacuna* and *Alia* give vigorous defensive responses to *Leptasterias*, *Notoacmea paleacea* gives no detectable flight response to the presence of this

predator, in striking contrast to the mushrooming flight behavior of many other limpets (Bullock, 1953; Feder, 1963; Feder, 1972). Yet, very few specimens of *N. paleacea* are consumed by the seastar. We suggest that *N. paleacea* has defenses that are entirely different from those of the other two gastropods. Specifically, we suggest that particular chemicals, flavonoids, present in *Phyllospadix* are incorporated by the limpet and serve as a chemical defense against predation, undoubtedly aided by the tight fit of the limpet's shell with the *Phyllospadix* blade. Flavonoids such as are found in *Phyllospadix* and in *N. paleacea* are thought not to be synthesized by animals, and their rare occurrence in animals usually can be traced to a plant in the animal's diet (reviews by Fox, 1976; Harborne, 1967). Incorporation of flavonoids by marine mollusks has not been reported previously, but a pigment thought to be a flavonoid has been reported in digestive gland, mantle tissue, and other organs of the terrestrial gastropod *Helix pomatia* (Kubista, 1950). The possible occurrence of flavones in the shell of *Cepaea nemoralis*, *Helix aspersa*, and *H. pomatia* also has been reported (Comfort, 1951). Although the occurrence of plant chemicals in the bodies of terrestrial herbivorous insects is a well-documented phenomenon (flavonoids: Morris and Thomson, 1963; Morris and Thomson, 1964; Harborne, 1967; cardiac glycosides; Rothschild, 1972; Rothschild and Reichstein, 1976; Brower, Brower, and Corvino, 1967; general reviews: Eisner, 1970; Whittaker and Feeny, 1971), we believe that this is the first reported parallel case in the ocean of flavonoids being incorporated by a monophagous, angiosperm-consuming, marine invertebrate.

The presence of specific plant chemicals such as flavonoids in *N. paleacea* could reduce predation in two ways. They might render the limpet distasteful, or they might chemically camouflage the limpet. Only the shell of the limpet contained appreciable amounts of flavonoid, however; the part of the animal that would be consumed by the seastar did not contain appreciable amounts. Location of the incorporated plant chemical(s) in the shell suggests that chemical camouflage may be the more likely possibility. Two additional sets of observations further support this contention. First, when a moving specimen of *Leptasterias* encounters a specimen of *N. paleacea* on a *Phyllospadix* blade, the seastar usually continues without pause to crawl over the limpet. The seastar does not recoil from the limpet, nor does it begin to attack it. The seastar simply seems not to have detected the limpet. Second, two red algae, *Melobesia mediocris* and *Smithora naiadum*, which are regarded by algologists to be epiphytes restricted to *Phyllospadix* and the eelgrass *Zostera* (Abbott and Hollenberg, 1976), also occur on the shells of *N. paleacea*. Since these algae presumably settle at a site based on specific cues identifying that site as *Phyllospadix* (or *Zostera*), settlement of these algae on shells of *N. paleacea* may indicate that the limpet's shells were identified as *Phyllospadix* by the settling algae. A similar misidentification by *Leptasterias* clearly would reduce predation on *N. paleacea*. Finally, the hypothesis of chemical camouflage in the limpet's shell also suggests a function for the one behavioral response that *N. paleacea* does give to contact with *Leptasterias*. Upon contact, the limpet withdraws its soft, body parts and clamps its shell down firmly, just as it does upon contact with a probe. Since the limpet's shell is shaped to fit the plant blade precisely, all the predator would encounter after initial contact with the limpet would be the chemically cryptic shell and *Phyllospadix*. The chemical crypsis suggested here against a marine, nonvisual predator seems to us to be a natural analog of better-known color camouflaging of terrestrial organisms in response to visual predators.

The defensive strategies of *Alia*, *Lacuna*, and *N. paleacea* differ considerably; however, the strategy of each is appropriate to the life-style and morphology of that particular gastropod. Although all three gastropods occur in *Phyllospadix* beds and all are responding to the same predator, *Leptasterias*, each gastropod is interacting with this predator under a different set of circumstances. *Alia* and *Lacuna* are widely distributed, occurring on low intertidal rocks and algae, as well as on *Phyllospadix*. Thus, these gastropods occur in a variety of habitats and their behavioral responses are effective in a variety of habitats. The direct and highly effective proboscis strike of *Alia* is a behavioral response that can be employed anywhere. Indeed, it seems so effective that *Alia* reacts very little to the seastar until actual contact is made, even though *Alia* is able to detect the predator from a distance. Since *Lacuna* does not have a long proboscis like that of *Alia*, obviously the defensive strategy of *Lacuna* must be different. The response that *Lacuna* gives upon contacting a seastar is to fall. Falling was found to be an effective means of fleeing from *Leptasterias* in *Phyllospadix* beds, and it would seem also to be effective in other habitats where *Lacuna* occurs. Similarly, rotation of the shell by *Lacuna*, which seemed to lessen the likelihood that tube feet would attach to the shell, would work equally well regardless of the substratum. In contrast to *Alia* and *Lacuna*, which are eurytopic species, *N. paleacea* is stenotopic. This limpet occurs only on *Phyllospadix*, and the limpet's defenses, which include a chemically-camouflaged, precisely-fitting shell, are adapted specifically for life on this plant. These defenses seem more appropriate to the limpet's lifestyle than a behavioral defense. Among archeogastropods, the most common sort of behavioral defense is flight. However, since *N. paleacea* is dependent on *Phyllospadix*, it would seem that flight from the plant could be as dangerous as the predator.

We thank Jonathan Poulton, Steven O'Dell, Stephen Loomis, John Crowe, Becky Jensen, Kate Madin, and Soren Brauner, all of the University of California, Davis (UCD), and Larry Madin and Roger Mann, of the Woods Hole Oceanographic Institution (WHOI) for biochemical advice, use of equipment, and insightful discussions and suggestions. Arthur Shapiro (UCD) stimulated our interest in allelochemicals. James Carlton (WHOI) read and thoroughly commented on the manuscript. We thank Cadet Hand for use of facilities at the Bodega Marine Laboratory. Special thanks are due to James Carlton for his field and moral support. Part of this work was supported by a Graduate Research Award from UCD to D. Fishlyn.

#### SUMMARY

1. In *Phyllospadix* beds of central California, the gastropods *Lacuna marmorata*, *Alia carinata*, and *Notoacmea paleacea* occur in abundance with the predatory seastar *Leptasterias hexactis*. All three gastropods have defensive adaptations that reduce the frequency of predation by this seastar.

2. *Lacuna* responds to waterborne chemicals ("scent") emanating from distant *Leptasterias* by rotating the shell through an arc of 360°, waving its cephalic tentacles, and increasing general activity. Upon contact with the predator, *Lacuna* flees by falling off the *Phyllospadix* blade.

3. *Alia* does not respond vigorously to the scent of distant specimens of *Leptasterias*. Upon contact with *Leptasterias*, *Alia* rears up on the posterior portion of the foot and then begins to run away. If contact with the seastar persists, the snail strikes at the seastar's tube feet with its proboscis.

4. *N. paleacea* does not give a behavioral defensive response to *Leptasterias*. Rather, this stenotopic limpet may be chemically camouflaged, and this camouflage, together with the limpet's precisely fitting shell, may reduce predation by *Leptasterias*. *Notoacmea paleacea* eats *Phyllospadix*, and at least one specific chemical from the plant, a sulphated flavonoid pigment, also is found in the shell of this limpet. Due to the presence of specific, host-plant chemicals in the shell of *N. paleacea*, *Leptasterias* may fail to detect the limpet against the chemical background of the host plant.

5. *Lacuna* is the most frequently consumed prey of *Leptasterias* in the *Phyllospadix* beds, yet 89% of the 75 encounters observed between *Lacuna* and *Leptasterias* in the field resulted in the successful escape of the prey. The defensive adaptations of *Alia* and *N. paleacea* seem to be even more effective, since these gastropods are consumed only rarely by *Leptasterias*.

## LITERATURE CITED

- ABBOTT, I. A., AND G. J. HOLLENBERG, 1976. *Marine Algae of California*. Stanford University Press, Stanford, California, 827 pp.
- ANSELL, A. D., 1969. Defensive adaptations to predation in the Mollusca. *Proc. Mar. Biol. Assn. India*, Symp. Series 3: 487-512.
- BARBOUR, M. G., AND S. R. RADOSEVICH, 1979.  $^{14}\text{C}$  uptake by the marine angiosperm *Phyllospadix scouleri*. *Am. J. Bot.*, 66(3): 301-306.
- BROWER, L. P., J. VAN Z. BROWER, AND J. M. CORVINO, 1967. Plant poisons in a terrestrial food chain. *Proc. Natl. Acad. Sci. U. S. A.*, 57(4): 893-898.
- BULLOCK, T. H., 1953. Predator recognition and escape responses of some intertidal gastropods in presence of starfish. *Behaviour*, 5: 130-140.
- CHIA, F.-S., 1966. Systematics of the six-rayed sea star *Leptasterias* in the vicinity of San Juan Island, Washington. *Syst. Zool.*, 15: 300-306.
- COMFORT, A., 1951. The pigmentation of molluscan shells. *Biol. Rev.*, 26: 285-301.
- DAYTON, P. K., R. J. ROSENTHAL, L. C. MAHEN, AND T. ANTEZANA, 1977. Population structure and foraging biology of the predaceous Chilean asteroid *Meyenaster gelatinosus* and the escape biology of its prey. *Mar. Biol.*, 39: 361-370.
- EISNER, T., 1970. Chemical defense against predation in arthropods. Pages 157-217 in E. Sondheimer and J. B. Simeone, Eds., *Chemical Ecology*. Academic Press, New York.
- FEDER, H. M., 1963. Gastropod defensive responses and their effectiveness in reducing predation by starfishes. *Ecology*, 44(3): 505-512.
- FEDER, H. M., 1972. Escape responses in marine invertebrates. *Sci. Am.*, 227: 92-100.
- FEDER, H. M., AND A. M. CHRISTENSEN, 1966. Aspects of asteroid biology. Pages 87-127 in R. A. Booloottian, Ed., *Physiology of Echinodermata*. Interscience, New York.
- FISHLYN, D. A., 1976. Observations on the natural history and morphological variation of *Notoacmea paleacea* on *Phyllospadix scouleri* and *P. torreyi* in northern California. *Anna. Rep. West. Soc. Malacologists*, 9: 16-17.
- FOX, D. L., 1976. *Animal Biochromes and Structural Colours*. Second ed. University of California Press, Berkeley. 433 pp.
- FRITCHMAN, H. K., 1961. A study of the reproductive cycle in California Acmaeidae (Gastropoda). Part II. *Veliger*, 3: 95-101.
- GEISSMAN, T. A., Ed., 1962. *The Chemistry of Flavonoid Compounds*. Macmillan Co., New York. 666 pp.
- HARBORNE, J. B., 1967. *Comparative Biochemistry of the Flavonoids*. Academic Press, London. 383 pp.
- HARBORNE, J. B., 1973. *Phytochemical Methods*. Chapman and Hall, London. 278 pp.
- HARBORNE, J. B., 1975. Flavonoid sulphates: a new class of sulphur compounds in higher plants. *Phytochemistry*, 14: 1147-1155.
- HARBORNE, J. B., T. J. MABRY, AND H. MABRY, Eds., 1975. *The Flavonoids*. Parts 1 & 2. Academic Press, New York. 1204 pp.
- HOFFMAN, D. L., AND P. J. WELDON, 1978. Flight responses of two species of intertidal gastropods (Prosobranchia: Trochidae) to sympatric predatory gastropods from Barbados. *Veliger*, 20: 361-366.

- KUBISTA, V., 1950. Flavones in *Helix pomatia* L. *Experientia*, **5**: 100.
- MABRY, T. J., K. R. MARKHAM, AND M. B. THOMAS, 1970. *The Systematic Identification of Flavonoids*. Springer-Verlag, Berlin. 354 pp.
- MACGINITIE, G. E., AND N. MACGINITIE, 1968. *Natural History of Marine Animals*. Second edition. McGraw and Hill Book Co., New York. 523 pp.
- MACKIE, A. M., AND P. T. GRANT, 1974. Interspecies and intraspecies chemoreception by marine invertebrates. Pages 105-141 in P. T. Grant and A. M. Mackie, Eds., *Chemoreception in Marine Organisms*. Academic Press, New York.
- MENGE, B. A., 1972. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.*, **42**: 25-50.
- MONTGOMERY, D. H., 1967. Responses of two haliotid gastropods (Mollusca), *Haliotis assimilis* and *Haliotis rufescens*, to the forcipulate asteroids (Echinodermata), *Pycnopodia helianthoides* and *Pisaster ochraceus*. *Veliger*, **9**: 359-368.
- MORRIS, S. J., AND R. H. THOMSON, 1963. The flavonoid pigments of the marbled white butterfly (*Melanargia galathea* Seltz). *J. Insect Physiol.*, **9**: 391-399.
- MORRIS, S. J., AND R. H. THOMSON, 1964. The flavonoid pigments of the small heath butterfly, *Coenonympha pamphilus* L. *J. Insect Physiol.*, **10**: 377-383.
- NISSEN, P., AND A. A. BENSON, 1964. Absence of selenate esters and "selenolipid" on plants. *Biochim. Biophys. Acta*, **82**: 400-402.
- PHILLIPS, D. W., 1975. Distance chemoreception-triggered avoidance behavior of the limpets *Acmaea (Collisella) limatula* and *Acmaea (Notoacma) scutum* to the predatory starfish *Pisaster ochraceus*. *J. Exp. Zool.*, **191**: 199-210.
- PHILLIPS, D. W., 1976. The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. *Oecologia*, **23**: 83-94.
- PHILLIPS, D. W., 1977. Avoidance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. *J. Exp. Mar. Biol. Ecol.*, **28**: 77-86.
- PHILLIPS, D. W., 1978. Chemical mediation of invertebrate defensive behaviors and the ability to distinguish between foraging and inactive predators. *Mar. Biol.*, **49**: 237-243.
- PRATT, D. M., 1974. Behavioral defenses of *Crepidula fornicata* against attack by *Urosalpinx cinerea*. *Mar. Biol.*, **27**: 47-49.
- ROTHSCHILD, M., 1972. Secondary plant substances and warning colouration in insects. Pages 59-83 in H. F. Van Emden, Ed., *Insect/Plant Relationships*. Symp. Royal Entomol. Soc. (London). Blackwells Scientific Pub., Oxford.
- ROTHSCHILD, M., AND T. REICHSTEIN, 1976. Some problems associated with storage of cardiac glycosides by insects. *Nova Acta Leopoldina*, Suppl. no. **7**: 507-550.
- SUTTON, J. E., 1975. Class Asteroidea. Pages 623-627 in R. T. Smith and J. T. Carlton, Eds., *Light's Manual, Intertidal Invertebrates of the Central California Coast*, Third ed. University of California Press, Berkeley.
- SWAIN, T., 1976. Flavonoids. Pages 166-206 in T. W. Goodwin, Ed., *Chemistry and Biochemistry of Plant Pigments*, Second Edition. Academic Press, London.
- SZAL, R. A., 1970. Distance chemoreception in a marine snail, *Tegula funebris*. *Ph.D. Dissertation, Stanford University*, 202 pp. Diss. Abstracts No. 70-18485.
- TEST, A. R., 1945. Ecology of California *Acmaea*. *Ecology*, **26**: 395-405.
- WHITTAKER, R. H., AND P. P. FEENY, 1971. Allelochemicals: Chemical interactions between species. *Science*, **171**: 757-770.
- YONGE, C. M., 1962. Ciliary currents in the mantle cavity of species of *Acmaea*. *Veliger*, **4**: 119-123.